Introduction to the Trilobites: Morphology, Ecology, Macroevolution and More

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Learning Goals and Pedagogy

This lab is designed for middle level General Science or Earth Science classes. The learning goals for this lab are the following: 1) to familiarize students with the anatomy and terminology relating to trilobites; 2) to give students experience identifying morphologic structures on real fossil specimens 3) to highlight major events or trends in the evolutionary history and ecology of the Trilobita; and 4) to expose students to the study of macroevolution in the fossil record using trilobites as a case study.

Introduction to the Trilobites

The Trilobites are an extinct subphylum of the Arthropoda (the most diverse phylum on earth with nearly a million species described). Arthropoda also contains all fossil and living crustaceans, spiders, and insects as well as several other extinct groups. The trilobites were an extremely important and diverse type of marine invertebrates that lived during the Paleozoic Era. They only lived in the oceans but occurred in all types of marine environments, and ranged in size from less than a centimeter to almost a meter across. They were once one of the most successful of all animal groups and in certain fossil deposits, especially in the Cambrian, Ordovician, and Devonian periods, they are extremely abundant. They still astound us today with their profusion of body forms (see Fig. 1). Trilobites are well represented in the fossil record because their sturdy exoskeletons, thicker and stronger (and harder to break) than the shell of a modern crab, fossilized easily. Further, being arthropods, they molted as they grew, such that every single trilobite was capable of leaving behind many, many exoskeletons that could become fossilized. Most of what we know about trilobites comes from the remains of their mineralized exoskeleton, and in fact the external shell does provide a lot of information about what the trilobite animal inside the shell looked like. Most notably, the eyes are preserved as part of the skeleton so we have an excellent idea about how trilobite eyes looked and operated. In addition, there are a few rare instances when not only the external shell but also the soft tissues of trilobites were preserved including their legs, gut, and antennae. Interestingly, while the external shell differs quite a lot across the different trilobite species the internal anatomy was more uniform over time.

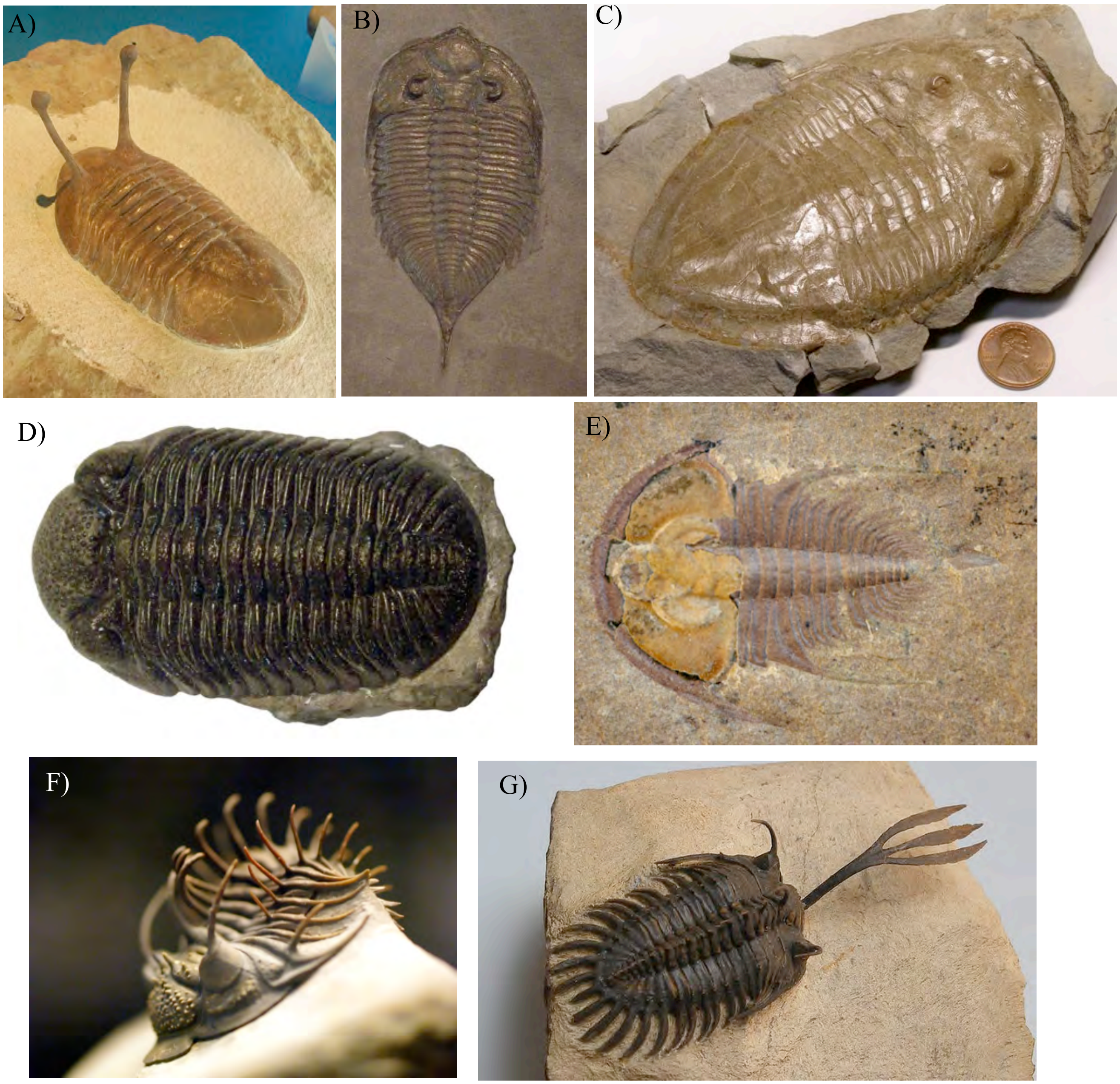


Figure 1: A) *Asaphus kowalewskii,* by Smokeybjb (Own work) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons, B) *Dalmanities limulurus* University of Kansas Museum, on exhibit, C) *Isotelus iowensis* University of Kansas Museum, Invertebrate Paleontology (KUMIP) 294608, D)*Phacops milleri* University of Kansas Museum, on exhibit, E) *Olenellus sp.* University of Kansas Museum, Invertebrate Paleontology (KUMIP) 369418, F) *Comura* sp., by Wikipedia Loves Art participant "Assignment_Houston_One" [CC-BY-SA-2.5 (http://creativecommons.org/licenses/by-sa/2.5)], via Wikimedia Commons*;* G) *Walliserops trifurcates*, by Arenamontanus (Own work) [CC-BY-2.0 (http://creativecommons.org/licenses/by/2.0/)], via Flickr.

Sheer Numbers

The sheer variety of trilobites is impressive. As mentioned above, they belong to the most diverse phylum, the arthropods, and when it comes to total variety and diversity trilobites were no slouches themselves. They have been divided into:

10 Orders that include 150 Families assigned to
~5,000 Genera that contain perhaps more than 20,000 Species

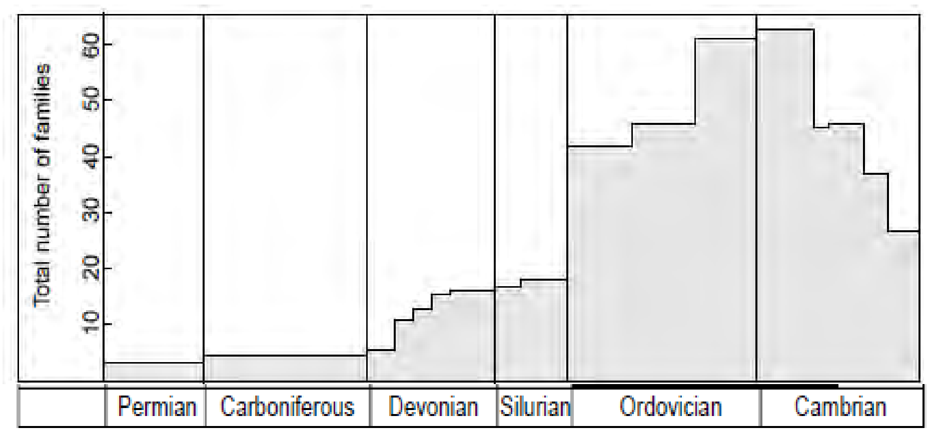


Figure 2: Diversity of trilobites, number of families, through time from the *Treatise on Invertebrate Paleontology*, used with permission.

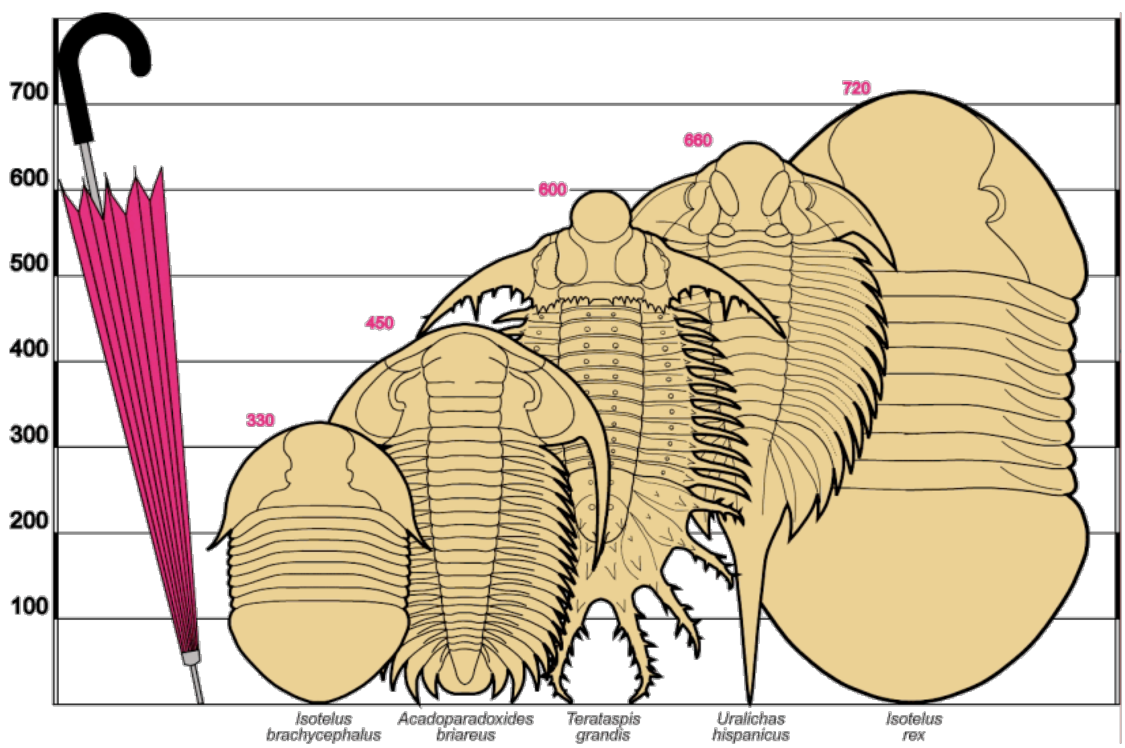


Figure 3: Size range of the largest trilobites, from Sam Gon's website, http://www.trilobites.info/lgtrilos.htm , used with permission.

As already mentioned, trilobites show an impressive variation in size, from under 1 mm to over 70 cm in length, although the average trilobite was probably around 5-6 centimeters. Figure 3 nicely illustrates the sizes of the very largest known trilobites compared to a full-sized umbrella.

Temporal and Spatial Distribution

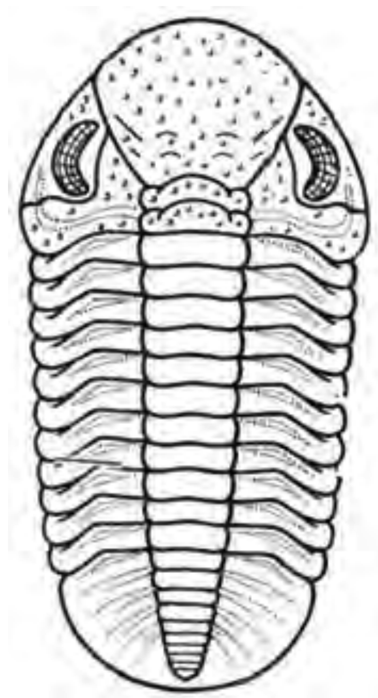
521 Ma (Cambrian) to 251 Ma (Permian) ≈ 300 million year history
Greatest numbers in Cambrian and Ordovician
Worldwide distribution

The earliest trilobites appear suddenly in rocks of Early Cambrian age (522-530 Ma) from present day Scandinavia and Eastern Europe. Soon afterwards trilobites also appeared in China, North America, Antarctica, and Australia and within the Early Cambrian are found throughout the world. The early history of trilobite evolution suggests that significant evolutionary changes took place in the Trilobita even before the earliest known fossilized examples. Current estimates suggest that although the earliest trilobites appeared in the fossil record around 525 Ma they may have originated 550-600 Ma (Lieberman and Karim, 2010). The reasons why the earliest relatives may have been absent from the fossil record remain unclear but may include the fact that they were small, lacked a hard shell, or they were very rare and restricted to environments where they were unlikely to fossilize.

The trilobites continued to diversify into the Ordovician, but were hit particularly hard by the mass extinction at the end of the period. Trilobites were able to partially recover after the end Ordovician mass extinction, only to be hit again by the Late Devonian mass extinction. Trilobite diversity failed to rebound after the Late Devonian event and the group was eventually wiped out during the largest mass extinction of all time at the end of the Permian. Indeed part of the reason trilobites are no longer with us today has to do with the fact that they fared particularly poorly during times of mass extinction (Lieberman and Melott, 2013).

General Anatomy

In small, lab station groups of 3 or 4 students, identify at least 5 shape-related (morphological) features of trilobites that you think are important to describing what a trilobite looks like to someone who has never seen one before. Mark the features on the trilobite diagram provided with lines pointing to each feature your group chooses to identify.



Look at the variety of body forms shown in Figures 1 and 3. Identify any additional morphological features on your group's diagram that you think may be important for distinguishing one group of trilobites from another.

The name trilobite refers to the fact that their body is made up of three longitudinal (along the length of the body) sections: the central section, known as the **axial lobe**; and the two lobes on either side of the axial lobe, known as the **pleural lobes (Figure 4 and 5)**. Trilobites are also separated into three sections from front to back known as tagmata: the **cephalon,** or head; the middle section made up of multiple segments known as the **thorax;** and the posterior (tail) section, or **pygidium** (plural = pygidia) **(Figures 4 and 5)**. Some trilobites have spines originating at the genal angle, in which case they are called **genal spines**.

Compare the morphological features identified by your group to the labeled trilobite diagrams used by paleontologists (Figure 4). How do the commonly accepted anatomical regions of trilobites compare with the important anatomical features that were identified by your group? Did you find the three longitudinal sections? How about the tagmata?

Now use the diagram and descriptions provided in Figure 4 to label the anatomical elements highlighted in this photograph of the trilobite *Phacops rana*.

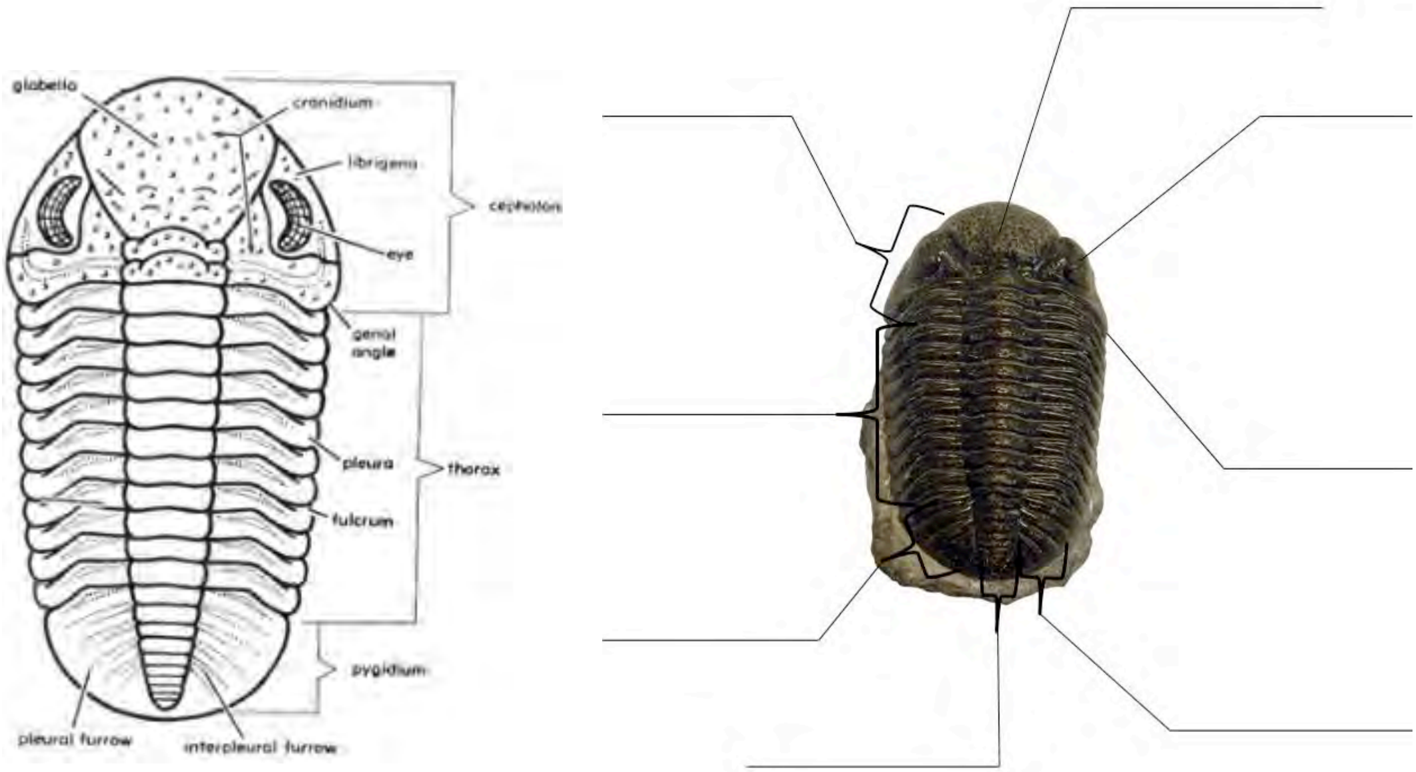
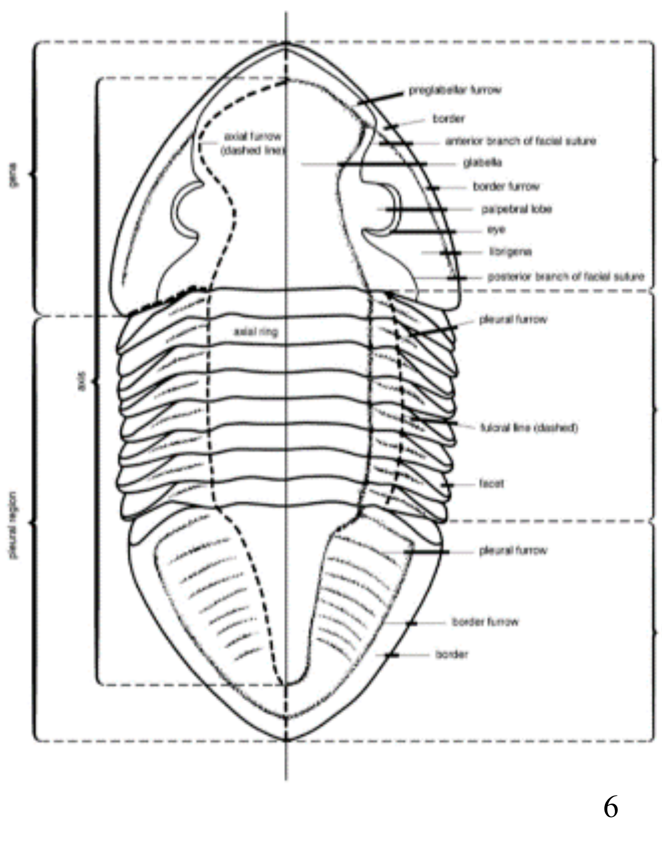


Figure 4: External trilobite anatomy. A) Diagram of *Phacops* from the *Treatise on Invertebrate Paleontology*, used with permission. B) Photo of *Phacops milleri* specimen from the University of Kansas Museum, on exhibit.

Next use the diagram and descriptions provided in Figure 5 to label some of the same anatomical elements in this photograph of the morphologically distinct *Isotelus sp*.



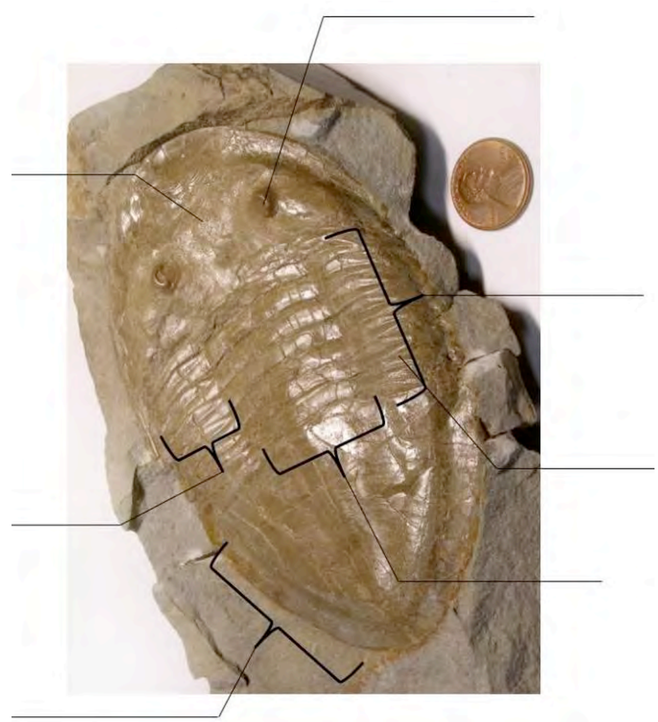


Figure 5 (previous page): External trilobite anatomy continued. A) Diagram of the Ordovician trilobite, *Isotelus* from *the Treatise on Invertebrate Paleontology*, used with permission. B) *Isotelus iowensis* University of Kansas Museum, Invertebrate Paleontology (KUMIP) 294608.

Now that you are familiar with general trilobite anatomy, choose any one of the Trilobites from Figure 1. Spend a few minutes writing a description of your trilobite, but <u>do not</u> indicate which one you chose. Try to be as detailed in your descriptions as you can, and try to use correct anatomical terminology where possible.

Once you have finished recording your observations, trade descriptions with another group and try to determine each other's chosen trilobite based on the written descriptions. You may not ask for clarifications and must rely solely on the written descriptions.

Were you able to match their description with the correct Trilobite? Yes / No

Were they able to identify your Trilobite? Yes / No

What was difficult about identifying the correct trilobite from the written descriptions?

What could make the task easier? How might you change your group's description to make it easier to identify the correct trilobite?

PART TWO – Ventral Anatomy & Eyes

The photos and diagrams we have looked at so far depict the **dorsal** (upper or backside) surface of the trilobite. Below is a diagram of the **ventral** (underbelly) morphology of a trilobite.

An important feature of the undersides of trilobites is a calcified plate near the mouth known as the **hypostome.** The hypostome is thought to have been used in feeding. It may be rigidly or flexibly attached, and can display a variety of shapes including points or fork-shaped projections.

Figure 6: Ventral view of a *Ceraurus whittingtoni* cephalon from the *Treatise on Invertebrate Paleontology*, used with permission.

The shells of trilobites are frequently preserved as fossils due to their mineralized exoskeletons hardened with calcite. Trilobite limbs, however, are rare in the fossil record because they lacked a hard mineralized coating of calcite. To reconstruct limb morphology, we must rely on exceptionally preserved trilobites, those preserving both hard and soft tissues as fossils. This *Triarthus eatoni* specimen (Fig. 6) is an example of a pyritized trilobite (the limbs are substituted by the mineral pyrite which contains Iron and Sulfur) that preserves soft tissues such as antennae and appendages. Trilobites have **biramous** appendages: each limb is made up of two branches. These branched limbs are found along the length of the body occurring in repeating pairs, with multiple pairs on the cephalon, one pair per thoracic segment, and several small pairs on the pygidium. Unlike many modern arthropods with many specialized limbs, the limbs of trilobites are essentially the same from front to back, varying only in size. The upper branch, or **gill** branch, is a soft, filamentous structure used to obtain oxygen from the water. The lower branch is a jointed walking leg used for locomotion. The gill branches are located directly under the trilobite shell.

Please answer the following questions using the diagrams and photos provided in Figure 7:

How many pairs of limbs does the cephalon (head) have?

How many pairs of limbs does the thorax have (hint, there are 14 throacic segments)?

On the diagrams or photo above (Fig. 7), draw a line separating the thorax from the pygidium (tail) (hint, the diagram showing the side view may be the most helpful for this task).

Does the pygidium (tail) have limbs? Y/N

A) B)

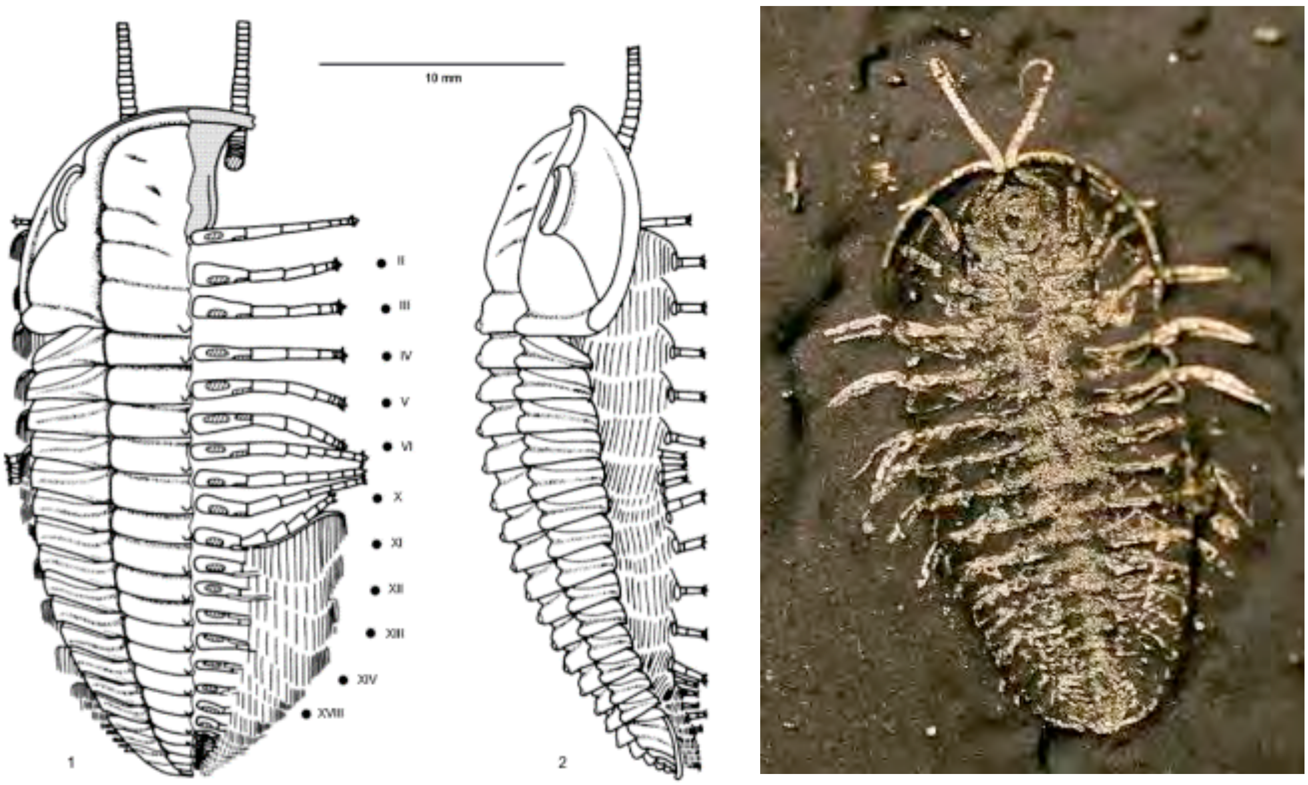
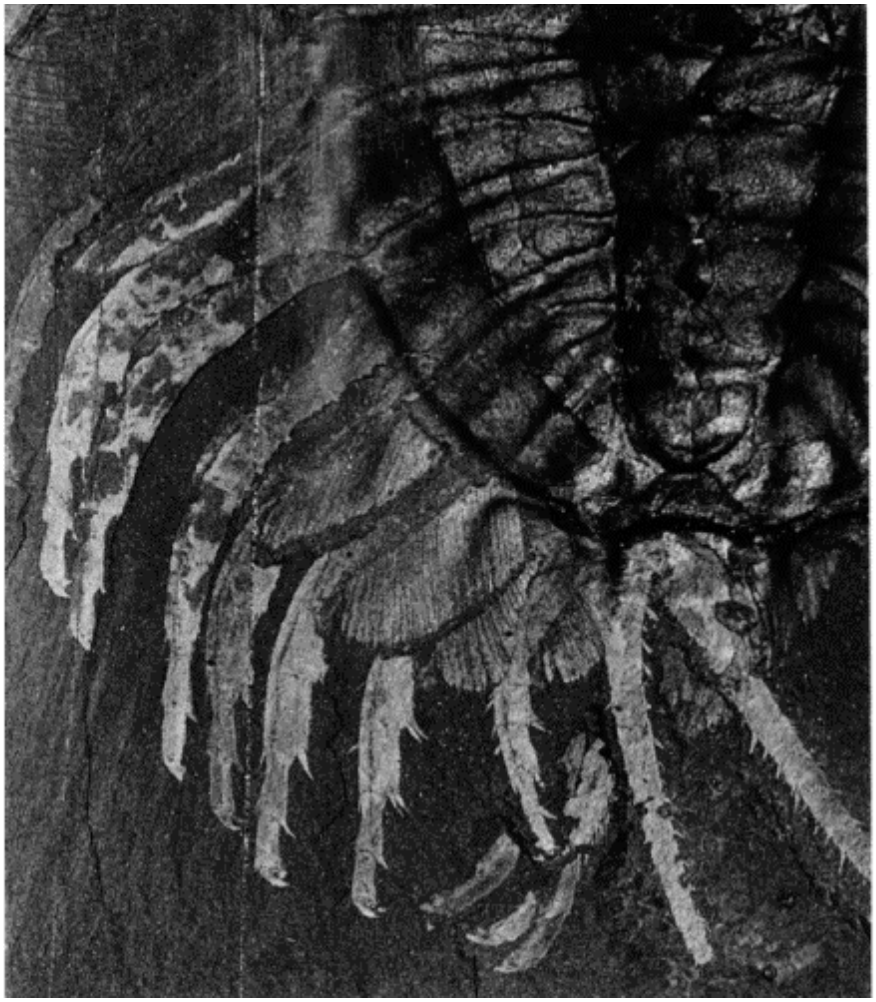


Figure 7: Limb morphology. A) Diagram of the limbs of *Triarthus eatoni* from the *Treatise on Invertebrate Paleontology*, used with permission. B) Photograph of a pyritized specimen of *Triarthus eatoni* YPM 219 from the Yale Peabody Museum collections, by Bruce Lieberman, used with permission.

Using the diagram as a guide, circle and label a walking leg and a gill branch on the close-up photo provided in Figure 8.

Explain why the gill has a feathery appearance? What was the gill's function?

A)



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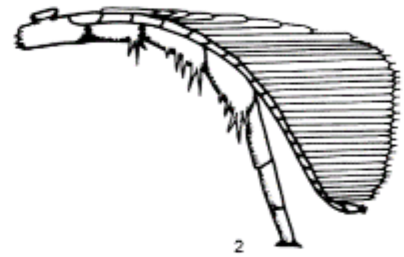


Figure 8: Enlarged view of trilobite biramous limb morphology showing the jointed walking leg and filamentous gill branch. A) Close up of Middle Cambrian *Olenoides serratus* from *Treatise on Invertebrate Paleontology*, used with permission. B) Limb reconstruction from the *Treatise on Invertebrate Paleontology*, used with permission.

Many different clades of trilobites are capable of flexing the thoracic segments to rest the cephalon on the pygidium. The process of flexing into a ball is known as **enrollment**. Some trilobites even have structures that allow the cephalon (head) and pygidium (tail) to interlock for a tight fit. The enrollment process is similar to what you may have observed in a rolly-polly or pill bug.

Figure 9: Fully enrolled trilobites, *Flexicalymene meeki* (Upper Ordovician) University of Kansas Museum, Invertebrate Paleontology (KUMIP) 241339-241344 and University of Kansas Museum, Invertebrate Paleontology (KUMIP) 241347-241349.

Given what you just learned about the structure of trilobite limbs, what do you think the benefit of enrollment was? What might cause a trilobite to roll up into a ball?

Eyes

Trilobite eyes are often preserved as part of the fossilized skeleton, and exhibit a wide variety of evolutionary adaptations. Trilobites had compound eyes, made up of numerous calcite lenses. Eyes in which individual lenses are not separated are known as **holochroal** (Fig. 10A). All of the lenses in a holochroal eye share a single (whole) cornea or covering. Eyes in which individual lenses were separated by exoskeleton material are known as **schizochroal** (Fig. 10B). In a schizochroal eye, each lens had its own (divided) cornea. Holochroal and schizochroal eyes may have both allowed trilobites to see static objects, but schizochroal eyes were better at detecting movement.

The holochroal style of eyes evolved first, whereas the schizochroal style of eyes evolved in only one group of trilobites, the Order Phacopida, and presumably evolved sometime in the Late Cambrian.

A) B)

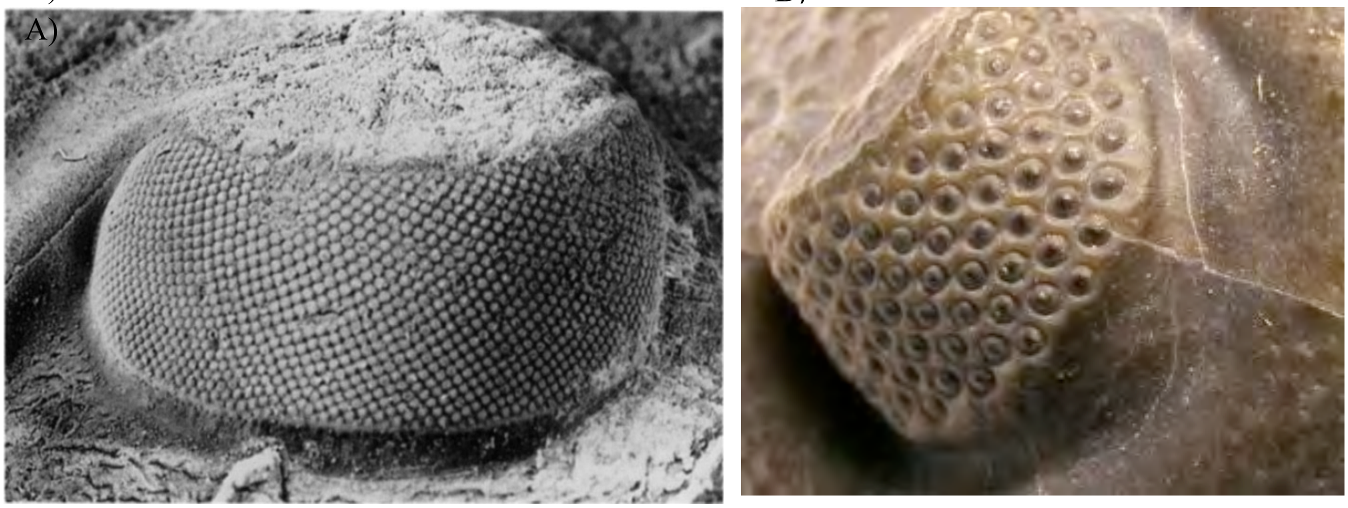


Figure 10: A) Holochroal eye of *Paralejurus brongniarti*, Devonian, Bohemia; lateral view, ×7 (Clarkson, 1975, pl. 1, fig. 1) from the *Treatise on Invertebrate Paleontology*, used with permission. B) Schizochroal eye of *Phacops rana* University of Kansas Museum, Invertebrate Paleontology (KUMIP) 240295.

Describe the visual capabilities of the trilobites in Figure 11. Things to consider: whether the eye is schizochroal or holochroal; the size of the eye; the position of the eye; and the field of vision the trilobite may have had (in which directions can the trilobite see)?

A) B) C) D)

Figure 11: A) *Erbenochile erbenii*, by Moussa Direct Ltd. (Own work) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons, B) *Ellipsocephalus hoffi,* by TheoricienQuantique (Own work) [Public domain], via Wikimedia Commons, C) *Asaphus kowalewskii,* by Smokeybjb (Own work) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons, D) *Phacops milleri* University of Kansas Museum, on exhibit.

A) **B)**

C) **D)**

PART THREE - Ecology

Ecological Niches

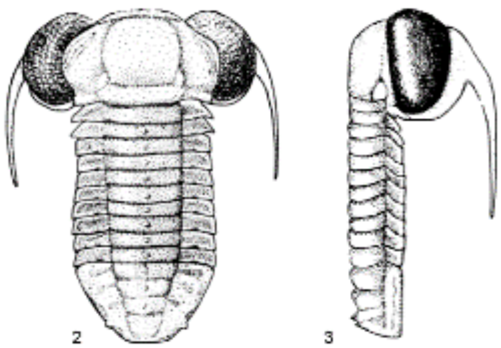
As mentioned above, trilobites are only found in rocks representing marine environments, but they were present at all depths and in all marine environments. Trilobites filled many different ecological niches and were capable of a wide range of behaviors. Paleontologists reconstruct these behaviors and modes of life using a combination of evidence including morphology, occurrence with other organisms, types of sediments in which trilobites are preserved (yielding information on the types of environments in which trilobites lived), and trace fossils or trackways made by trilobites. Below are some examples of morphological traits exhibited by trilobites, scientific interpretations of those traits, and the lifestyle or behavior inferred from the interpretations.

Fossil Evidence	**Interpretation**	**Inferred Lifestyle or Behavior**
Reduced thorax and pygidium; smooth cephalon; downward projecting spines; occurs in many types of rocks	Light, streamlined body allows fast swimming. Spines prohibit effective movement on the sediment surface. Distribution controlled by water column characteristics rather than sediment characteristics.	Pelagic Lifestyle/Swimming
Smooth exterior, broad & flat axial lobe Larger muscle attachments	Reduce friction Stronger limb motions to move sediments	Burrowing
Eyes reduced or absent Whip-like pygidium Wide bodies, genal spines	Darker conditions, less need for keen eyesight, able to swim Added support for soupy substrate	Living in Deep Water
Well developed limbs, flexible hypostome, trilobite feeding traces, called *Cruziana*	Food passed anteriorly towards the mouth during the course of movement, flexible hypostome used as a scoop.	Particle Feeding
Unusual occipital angle, pitted fringe	Pits allow water to flow through cephalon from leg-generated currents	Filter Feeding
Rigid hypostome; hypostome with forked projections	Ability to process relatively large food particles	Predatory, feeding on soft bodied worms

Now try this matching exercise. Using information from the above chart and looking carefully at the 6 trilobites shown in Figure 12, classify each fossil A – F in Figure 12 with their inferred lifestyle listed below (numbers 1-6).

A) *Lloydolithus lloydi*

B) *Carolinites genacinaca*



C) *Asaphus lepidurus*

D) *Cruziana* trace fossil

E) *Ampyx priscus*

F) underside *Asaphus expansus*

1) Deep water _______
2) Particle feeding _______
3) Filter feeding _______
4) Predatory _______
5) Pelagic _______
6) Burrowing _______

Figure 12: A) *Lloydolithus lloydi*, by Tomleetaiwan (Own work) [CC0], via Wikimedia Commons, B) *Carolinites genacinaca*, from the *Treatise on Invertebrate Paleontology*, used with permission, C) *Asaphus lepidurus*, by DanielCD (Own work) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons, D) *Cruziana* trace fossil, by Luis Fernández García (Own Work) [CC-BY-SA-2.1-Es (http://creativecommons.org/licenses/by-a/2.1/es/deed.en)], via Wikimedia Commons, E) *Ampyx priscus,* by Dwergenpaartje (Own work) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons, F) Ventral view of *Asaphus expansus*, by Dwergenpaartje (Own work) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons.

PART FOUR: Evolution

Review of Selected Trilobite Orders

Order Agnostida (Fig. 13) – Early Cambrian to Late Ordovician, abundant and widespread. Agnostoids are typically small (only a few mm long) and **isopygous**, having a cephalon and pygidium that are similar in both outline and size. Agnostid trilobites are frequently blind. Their thorax consists of only 2-3 segments. The limbs of Agnostoids, known only from juveniles, are morphologically very different from the limbs of other trilobites. This major difference in limb morphology has cast doubt on the placement of the Agnostoids within the class Trilobita and several authors believe the Agnostoids should lie just outside of the Trilobita. The agnosticism about their true relationship to trilobites explains their distinctive name.

Figure 13: Photo of the Agnostoid trilobite *Anglangostus* from the *Treatise on Invertebrate Paleontology*, used with permission.

Order Redlichiida (Fig. 14) – Early to Middle Cambrian, the earliest order of trilobites including the Olenelloidea, Emuelloidea, Redlichioidea, and Paradoxidoidea. Redlichiids possess primitive morphological characters including numerous thoracic segments, spiny tips at the end of their thoracic segments, and **micropygy** – a small pygidium relative to body size made up of a small number of fused segments.

Figure 14: *Olenellus sp.* specimens, A) University of Kansas Museum, Invertebrate Paleontology (KUMIP) 86258 and B) University of Kansas Museum, Invertebrate Paleontology (KUMIP) 369418.

A) B)

Order Phacopida (Fig. 15) – Early Ordovician to Middle Devonian. Phacopoids are large bodied and extremely diverse in their morphology. Members of the Phacopida are united by their distinctive, schizochroal eyes. Suborders include Calymenina, Phacopina, Cheirurina. This order also includes the subfamily Asteropyginae shown below.

A) B)

Figure 15: A) *Walliserops n. sp*., by Moussa Direct Ltd. (Moussa Direct Ltd. image archive) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons. B) *Paraceraurus*, by Vassil (Alias Collections.) [GFDL (http://www.gnu.org/copyleft/fdl.html) or CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons.

Macroevolution of the Trilobites

Macroevolution is the study of the patterns and processes that affect the birth, death, and persistence of species. For instance, scientists who study macroevolution might wonder when and why new species arise or why some groups speciate (form new species) rapidly while others give rise to new species very slowly. Ultimately, macroevolution is the study of evolution at the large scale.

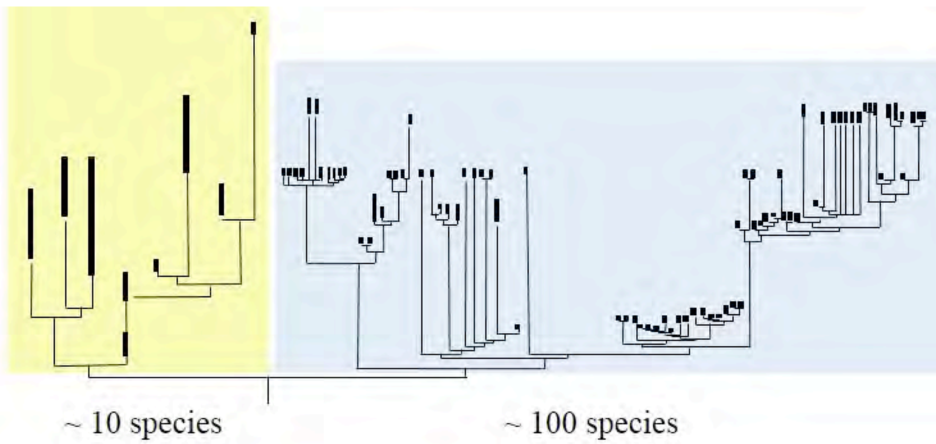


Figure 16: Two clade (yellow and blue) within the same group that show very different patterns of diversity. The yellow clade has few long-lived species while the blue clade has many more short lived species.

Questions of interest to scientists studying macroevolution might include:

1) Why are some groups of organisms (clades) diverse while others have only a few species within them?
2) Are there certain trends in the evolution of a particular group over time?
3) How are different groups affected by mass extinctions?

For example, the trilobites appear to be harder hit by mass extinctions than their contemporaries (Lieberman and Karim, 2010). In spite of their high levels of diversity, trilobites suffered major losses during the end Ordovician and Late Devonian mass extinctions. After the Late Devonian biodiversity crisis, trilobite diversity failed to fully recover and the group was wiped out completely during the largest mass extinction of all time at the end of the Permian (Fortey and Owens, 1997).

Why do the trilobites thrive in normal background conditions yet remain more susceptible to mass extinctions than other types of organisms? To evaluate this question we need to consider the following:

Origination is the appearance of new species. Origination rate is measured as the number of new species appearances over a period of time.

Extinction is the permanent and global disappearance of a species. Extinction rate is measured as the number of species disappearances over a period of time.

Originations and extinctions constantly occur throughout geologic history. The small and relatively consistent rate of extinction happening under normal conditions is known as **background extinction**. When the extinction rate spikes, resulting in a large number of species going extinct at the same time, these events are identified as **mass extinctions**. Under normal conditions, groups that show high rates of speciation over time (many originations) are likely to also have high rates of extinction. This correlation leads us to our next concept, volatility.

Volatility is a measure of a group's stability through time and is a function of background origination and extinction rates. High volatility clades have high rates of extinction and origination, which can lead to the frequent turnover of species within the group. Low volatility groups have low rates of origination and extinction, leading to a stable clade made up of the same species over long periods of time. Volatility has been decreasing through time because high volatility groups have an increased probability of their diversity falling to zero, a value from which they can never recover (Lieberman and Melott, 2013). Lieberman and Melott (2013) describe this increased risk of clade-wide extinction as resulting in a "survival of the blandest" pattern as high volatility clades are weeded out over time while low volatility clades persist. The impacts of volatility seem to be particularly important during times of mass extinction, with high volatility clades, like ammonites and trilobites, suffering greater losses than their low-volatility contemporaries (Lieberman and Karim, 2010). Interestingly, the reason trilobites, and also ammonites are no longer with us today, is likely because they evolved rapidly. It was the same factors that made them evolve rapidly, however, that made them prone to extinction.

Lab Activity: (small student groups of 3 or 4)

Materials (per group): a poster board, markers, scissors.
assorted pasta (spaghetti, fettucini, lasagna, etc.) (~25cm long = ~10 million years).
assorted licorice ropes, (~5cm long = ~2million years).

Using the materials provided by your teacher and the lineages in Fig. 16 as a guide, create a poster model showing a high or a low volatility clade of trilobites. Use pasta to represent long-lived trilobite species or licorice for short-lived species. Include a brief description of your clade's attributes. Things to keep in mind: How diverse is your clade likely to be? How likely are the species to be long lived? What can you say about species turnover in this group?

Please draw a diagram of an example trilobite species from your hypothetical clade on your group's poster.

How could the physical (anatomical) features of your group's sample Trilobite have helped it to survive the ecological conditions in which it found itself?

After each group has presented their clade poster to the class please discuss/answer the following questions:

Which group's clade model had the highest rate of origination over time?

Which group's clade model had the highest rates of extinction over time?

Which group's clade model was the most stable (least volatile)? Does the most stable group also have the longest history?

Which group's clade do you expect to have survived the longest? Explain your choice.

Is it possible to build up high diversity in a low volatility clade? If so, how might it occur?

Why do you think that pasta was provided to represent the longer-lived species of trilobites and licorice for the shorter lived ones? Hint: Which is blander and which would you rather eat and why?

References

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